



Tree species diversity promotes soil carbon stability by depressing the temperature sensitivity of soil respiration in temperate forests

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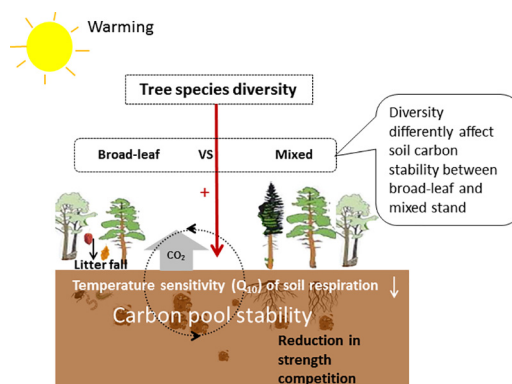
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HIGHLIGHTS

- Tree species diversity affects the temperature sensitivity of soil respiration.
- Higher species diversity leads to lower Q_{10} for both broad-leaf and mixed stands.
- Spatial variation of soil respiration is independent of tree species diversity.
- Diversity affects soil C stability differently in broad-leaf and mixed stands.

GRAPHICAL ABSTRACT



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ABSTRACT

The diversity-stability interrelationship suggests that high diversity can buffer fluctuations in environmental conditions such as temperature; we thus hypothesize that tree species diversity will lower the temperature sensitivity of soil respiration (R_s), known as Q_{10} value. Our hypothesis was tested in a deciduous broad-leaf and a coniferous-broad-leaf mixedwood stand in the warm temperate region in China. We measured soil respiration and indices of tree species diversity including species richness (S), the Berger-Parker index (d), the Simpson index (λ), the Shannon index (H_e'), and the Pielou evenness index (J_e). Our results generally confirm our hypothesis that Q_{10} was positively correlated to λ , but negatively related to H_e' , d , and J_e , and independent of S , in both stands. However, R_s was independent of the diversity indices. These findings imply that tree species diversity promotes soil carbon stability by depressing the Q_{10} . Furthermore, different biotic and abiotic variables explained the variations of species diversity and Q_{10} in the broad-leaf and mixedwood forests, suggesting that the mechanisms underlining the effects of tree species diversity on Q_{10} are different between the two forest types. We conclude that sustainable forest management that improves tree species diversity will increase soil carbon stability and benefit our efforts to mitigate climate change.

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1. Introduction

Rapid species loss worldwide (Rockstrom et al., 2009) and its potential effects on ecosystem services stimulate the study of relationships between biodiversity and ecosystem function (Loreau et al., 2001; Tilman et al., 2014). Evidence shows that biodiversity increases ecosystem stability in a changing environment (Tilman et al., 2006; Jiang and Pu, 2009; Hector et al., 2010), while the mechanisms that underlie this effect are still poorly understood (Loreau and de Mazancourt, 2013). As one of the most important functions of ecosystems, soil carbon (C) sequestration has been widely studied (Trumbore et al., 1996; Lal, 2004; Davidson and Janssens, 2006). The change in vegetation composition or biodiversity degradation has been also demonstrated to exert a significant impact on both short-term C fluxes (Ward et al., 2009) and long-term soil C storage (Augé, 2001; Norby and Zak, 2011; Lange et al., 2015). Thus, studies on the relationship between soil processes and biodiversity (Nielsen et al., 2011; Bardgett and van der Putten, 2014), and the connections among plants, soil biota and soil C storage (Averill et al., 2014; Lange et al., 2015) have been explored to some extent. However, the linkage between species diversity and the stability of soil carbon has been rarely documented.

Soil CO₂ efflux, also known as soil respiration (R_s), the second largest terrestrial carbon flux (Raich and Potter, 1995), was related to species diversity in grasslands (Stocker et al., 1999; Wardle et al., 1999; Dias et al., 2010). In temperate and boreal forests, tree species are believed to influence the size of soil carbon stocks (Vesterdal et al., 2013), and the effect of tree species diversity on R_s has been tested in monocultural and mixed species stands (Murphy et al., 2008). The temperature dependence of R_s , known as Q_{10} value (Van't Hoff, 1898), has been widely used to address the sensitivity of soil CO₂ flux to temperature variation (Davidson et al., 2006). Large variability of Q_{10} values has been reported between ecosystems (Fierer et al., 2005; Peng et al., 2009), inter-annually (Xu and Qi, 2001; Chen et al., 2010), and spatially within stands (Tang and Baldocchi, 2005; Khomik et al., 2006; Metcalfe et al., 2008; Luan et al., 2013). Due to the complexity of factors affecting soil CO₂ flux, contradictory relationships between Q_{10} and the quality of soil organic carbon have been reported, where similar (Fang et al., 2005; Reichstein et al., 2005a, 2005b) or different (Fierer et al., 2005; Conant et al., 2008; Hartley and Ineson, 2008) temperature sensitivities of soil organic matter with a different quality have been debatable. Our previous work illustrated that the spatial variation of Q_{10} values can be partially attributed to the lability of soil organic carbon (Luan et al., 2013). Given that Q_{10} value is a comprehensive parameter that reflects the soil CO₂ flux, it is an important soil property to predict possible feedbacks between the global carbon cycle and the climate system (Davidson et al., 2006). In this study, we aim at answering if there is a linkage between tree species diversity and soil carbon stability, by evaluating how R_s responds to temperature change.

According to the stabilization effects of biodiversity on ecosystem characteristics, we hypothesize that tree species diversity can be a buffer against fluctuations in environmental conditions, such as temperature, on R_s , and high tree species diversity will decrease the Q_{10} , which means that greater tree species diversity will reduce the sensitivity of soil CO₂ efflux to climate warming. Taking advantage of a large dataset on calculated Q_{10} values based on field measurements and the associated tree species diversity data of forest stands, we tested our hypothesis in a regenerated oak forest (deciduous broad-leaf trees, hereafter referred to as a broad-leaf stand) and a pine plantation with some broadleaf species voluntarily regenerated due to the lack of management (coniferous and broad-leaf mixed species trees, hereafter referred to as a mixed stand) in a warm temperate region in China. This study intends to provide important implications of sustainable forest management in terms of soil carbon stability.

2. Materials and methods

2.1. Study site and experimental design

The study site was located at the Forest Ecological Research Station in Baotianman Natural Reserve (111°47'–112°04'E, 33°20'–33°36'N), Henan Province, China. The study site has an annual mean precipitation of 900 mm and air temperature of 15.1 °C. Upland soils are dominated by Haplic luvisol (FAO) developed on granite. In this study, a regenerated oak stand (a broad-leaf stand, 40–50 years old) and a nearby pine plantation without intensive management for about 40 years (mixed stand) were used to test our hypothesis. The broad-leaf stand was dominated by *Quercus aliena* Bl. var. *acuteserrata* Maxim. ex Wenz., which accounts for 33% of the trees, with other tree species including *Carpinus cordata* Bl., *Cornus controversa* Hemsl., *Tilia tuan* Szyszyl., and *Carpinus turczaninowii* Hance. The mixed stand was dominated by *Pinus armandii* Franch., but some broadleaf species were also voluntarily regenerated due to the lack of management; such species include *Quercus aliena* var. *acuteserrata*. The sub-canopy contained 22 woody species, of which *Dendrobenthamia japonica* var. *chinensis* Fang, *Lindera obtusiloba* Bl., *Carpinus cordata* Bl., and *turczaninowii* Hance were the most common. International Code of Nomenclature for the species was used in this paper.

One 60 × 80 m block was delineated in each stand. Within each block, 10 × 10 m square grids were systematically laid out and 35 subplots (1 × 1 m) were set up at the intersections of these grids for measuring R_s . Tree species was identified and each tree with a diameter at breast height (DBH) larger than 1 cm was recorded and with its location in the plot mapped to calculate the indices of tree species diversity.

2.2. R_s , microclimate measurements, and Q_{10} calculation

We installed PVC collars (19.6 cm inside diameter) in each subplot in September 2008 and the PVC collars were kept on the site throughout the study. Soil respiration measurements were conducted for a total of 12 and 13 measurement campaigns for the broad-leaf and mixed stands, respectively, using a Li-8100 soil CO₂ flux system (LI-COR Inc., Lincoln, NE, USA), from October 2008 to October 2009, in the snow-free period. Sampling was performed between 9:00 and 15:00 (GMT + 8:00). Soil temperature at the 5 cm depth (T_5) was measured adjacent to each respiration collar with a portable temperature probe that is attached to the Li-8100.

An exponential equation was used to describe the temporal relationship between R_s and T_5 for each subplot:

$$R_s = ae^{bT_5} \quad (1)$$

Table 1

Descriptive statistics for tree species diversity indices (within 5 m of measurement points) and soil respiration.

	Broad-leaf stand			Mixed stand		
	Mean	S.D.	Range	Mean	S.D.	Range
R_s ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ^a	2.12	0.58	1.16–4.17	2.01	0.44	1.07–3.16
Q_{10} ^a	3.8	0.95	1.7–5.12	4.25	0.81	2.30–6.21
d	2.54	1.07	1.05–6.00	2.49	0.86	1.17–4.75
λ	0.28	0.19	0.00–0.90	0.27	0.14	0.06–0.73
H_e'	1.34	0.42	0.20–2.03	1.42	0.43	0.51–2.33
J_e	0.82	0.15	0.29–1.00	0.82	0.09	0.46–0.94
S	5.23	1.68	2.00–9.00	6.03	2.31	2.00–12.0

^a Data from Luan et al. (2012).

Table 2Pearson correlation coefficients between tree species diversity indices and Q_{10} values when the diversity indices were calculated with different plot sizes.

Tree species diversity indices	Radius								
	2 m	3 m	4 m	5 m	6 m	7 m	8 m	9 m	10 m
Broad-leaf stand									
d	0.36*	−0.11	0.12	−0.31*	−0.33*	−0.32*	−0.31*	−0.38*	−0.32*
λ	−0.06	0.05	0.03	−0.28	0.33*	0.33*	0.37*	0.39*	0.37*
He'	0.11	−0.07	−0.01	−0.23	−0.30*	−0.30*	−0.38*	−0.40*	−0.38*
Je	0.44*	−0.11	−0.22	−0.28	−0.32*	−0.35*	−0.36*	−0.36*	−0.32*
S	0.28	−0.01	0.06	−0.10	−0.13	−0.14	−0.19	−0.25	−0.23
Mixed stand									
d	0.06	−0.26	−0.24	−0.29*	−0.42**	−0.51**	−0.47**	−0.54**	−0.57**
λ	−0.07	0.29*	0.06	0.27	0.39*	0.45**	0.44**	0.53**	0.54**
He'	−0.002	−0.29*	−0.11	−0.23	−0.36*	−0.41**	−0.38*	−0.48**	−0.48**
Je	0.18	−0.01	−0.31*	−0.29*	−0.39*	−0.45**	−0.53**	−0.61**	−0.61**
S	0.05	−0.31	−0.11	−0.16	−0.20	−0.25	−0.21	−0.27	−0.23

* Significance at $P < 0.05$.** Significance at $P < 0.01$.

where R_s is soil respiration; T_5 is soil temperature at 5 cm depth; and a and b are fitted parameters. The temperature sensitivity parameter, Q_{10} , of each subplot was calculated as:

$$Q_{10} = e^{10b} \quad (2)$$

2.3. Soil properties, root biomass, and tree species diversity indices

Soil samples were collected from the top 5 cm of the mineral soil for each subplot for measurements of soil organic carbon (SOC), total nitrogen (TN), and light fraction organic carbon (LFOC). The LFOC was obtained following the density fractionation method by Six et al. (1998), but using a CaCl_2 solution with a density of 1.5 g mL^{-1} (Garten et al., 1999). In August 2009, roots were extracted from fresh soil samples collected by two cores (10 cm diameter) from the 0–30 cm depth from each subplot. The coarse (>5 mm), medium (2–5 mm) and fine (<2 mm) roots were manually separated and their dry biomass (70 °C, 24 h) was then determined.

Based on the position and species data, we calculated diversity indices for stands within radius of 2–10 m of each measurement point of R_s :

Tree species richness:

$$S = \text{number of species in a plot} \quad (3)$$

Berger-Parker index (Berger and Parker, 1970):

$$d = 1/n_{\max}/N \quad (4)$$

Simpson index (Simpson, 1949):

$$\lambda = \sum_{i=1}^S P_i^2, P_i^2 = \frac{n_i(n_i-1)}{N(N-1)} \quad (5)$$

Shannon index (Shannon, 1948):

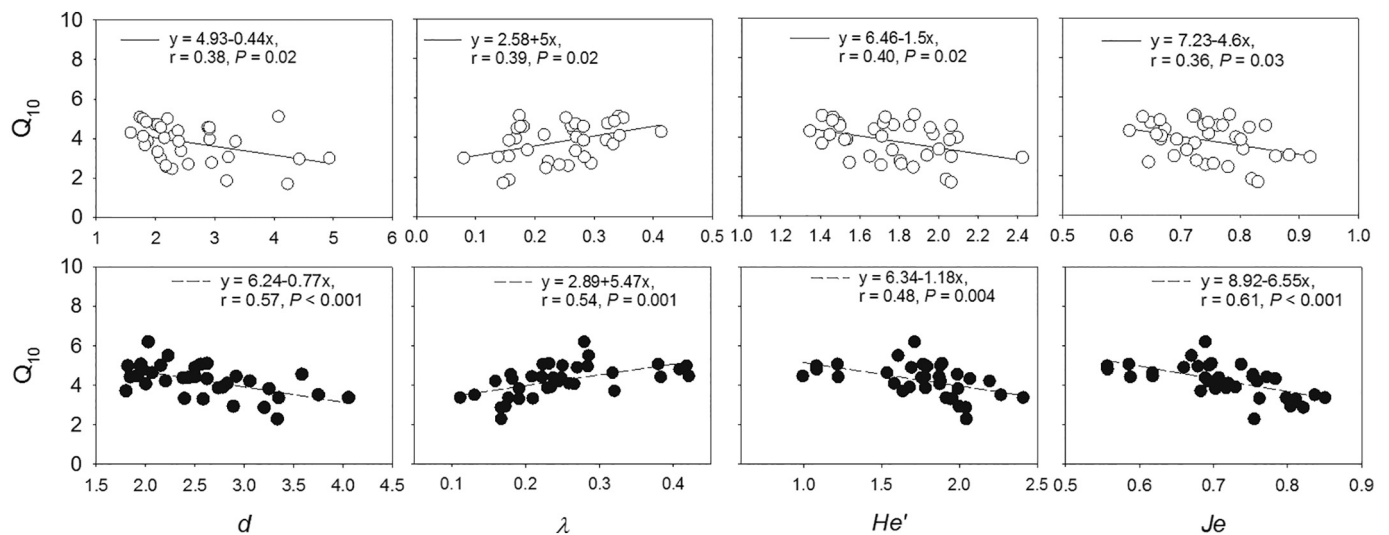


Fig. 1. Relationships between tree species diversity indices and Q_{10} values for the broad-leaf stand. Diversity indices were calculated for an area with a radius of 9 m (upper panel). Relationships between tree species diversity indices and Q_{10} values for the mixed stand, diversity indices were calculated for an area with a radius of 10 m (lower panel).

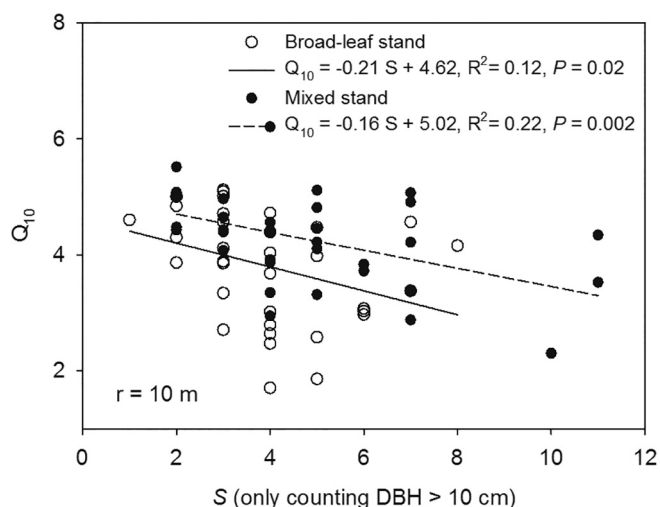


Fig. 2. Relationships between Q_{10} and S when only individuals with a DBH > 10 cm were included for the calculation for the broad-leaf ($r = 10$ m) and mixed stands ($r = 10$ m).

$$H'_e = -\sum_{i=1}^S P_i \ln P_i, P_i = \frac{n_i}{N} \quad (6)$$

and Pielou evenness index (Pielou, 1966):

$$J_e = \frac{H'_e}{H'_{\max}}, H'_{\max} = \ln S \quad (7)$$

where n_{\max} is the number of the most appeared species; n_i is the number of species (i); N is the sum of the individual numbers of all species.

For tree species diversity indices, d is the degree of the dominance of the most common species, which means that a plot having a higher species diversity corresponds to a higher d value; λ represents the homogeneous probability, where a plot having a higher species diversity corresponds to a lower λ value; H'_e quantifies the entropy (uncertainty or information content); and J_e indicates the evenness of a community, where a plot having a higher species diversity corresponds to both higher H'_e and J_e values.

2.4. Statistical analysis

The spatial variability of Q_{10} values was quantified by the semivariance [$\gamma(h)$], following Luan et al. (2012). Geostatistical analyses were performed with GS+ (Geostatistics for the Environmental Sciences, v.5.1.1, Gamma Design Software, Plainwell, MI). The analyses showed that Q_{10} values were spatially independent (data not shown), this allowed us to treat our measurement locations as independent samples for inferential statistics.

Pearson correlation analysis was performed to assess relationships among Q_{10} values, soil variables and tree species diversity indices for each stand ($n = 35$). Statistical analyses were conducted using SPSS version 21.0 (IMB SPSS Statistics, USA).

3. Results

3.1. Spatial variation of tree species diversity, R_s , and Q_{10}

High spatial variations of tree species diversity were observed in both the broad-leaf and the mixed stands. For example, within 5 m of the R_s measurement point, d values ranged from 1.05 to 6.0 for the broad-leaf stand, and from 1.17 to 4.75 for the mixed stand in the 35 subplots (Table 1). The tree species richness was between 2 and 9 for the broad-leaf stand, and between 2 and 12 for the mixed stand (Table 1). Similarly, both R_s and the Q_{10} values also presented high spatial variations for both forests (Table 1). Soil moisture was positively correlated with tree species diversity (Table S1, take He' for example), and negatively correlated with R_s (Fig. S1). However, no significant correlation between soil moisture and Q_{10} was detected (Fig. S1).

3.2. Dependence of Q_{10} variability on tree species diversity

Negative correlations between Q_{10} and tree species diversity indices including d , He' , and J_e , and positive correlations between Q_{10} and λ were observed in both broad-leaf and mixed stands (Table 2, e.g., Fig. 1). Significant correlations between diversity indices and Q_{10} existed when a radius of 6 m or greater was used for diversity assessment in both stands (Table 2). However, tree species richness (S) did not show significant relationships with Q_{10} in either stand (Table 2); nevertheless, species richness was negatively correlated with Q_{10} for both stands if only including trees with DBH > 10 cm (Fig. 2). In contrast, tree species diversity indices seldom explained the spatial variation of R_s in either stand (Table 3). When examining the mechanism underlining the effect of tree species diversity on Q_{10} , we found that the proportion of labile organic carbon to SOC, i.e., LFOC/SOC, significantly affected the variation of Q_{10} and was negatively correlated with tree species

Table 3

Pearson correlation coefficients between tree species diversity indices and R_s when the diversity indices were calculated with different plot sizes.

Tree species diversity indices	Radius								
	2 m	3 m	4 m	5 m	6 m	7 m	8 m	9 m	10 m
Broad-leaf stand									
d	−0.05	−0.16	−0.26	−0.19	−0.15	−0.15	−0.14	−0.05	−0.08
λ	0.01	0.23	0.22	0.22	0.20	0.21	0.22	0.14	0.17
H_e'	−0.14	−0.03	−0.20	−0.20	−0.15	−0.18	−0.18	−0.08	−0.12
J_e	0.05	−0.19	−0.13	−0.27	−0.27	−0.19	−0.22	−0.16	−0.17
S	−0.15	−0.01	−0.16	−0.18	−0.09	−0.08	−0.08	0.01	−0.03
Mixed stand									
d	0.28	−0.38*	−0.07	0.11	0.02	−0.02	0.03	−0.04	−0.06
λ	−0.36	0.34*	−0.09	−0.32*	−0.21	−0.18	−0.16	−0.09	−0.07
H_e'	0.32	−0.32*	0.06	0.30*	0.17	0.18	0.16	0.13	0.15
J_e	0.17	−0.34*	0.18	0.11	0.01	−0.10	0.01	−0.05	−0.01
S	0.27	−0.23	0.08	0.27	0.18	0.19	0.18	0.18	0.27

* Significance at $P < 0.05$.

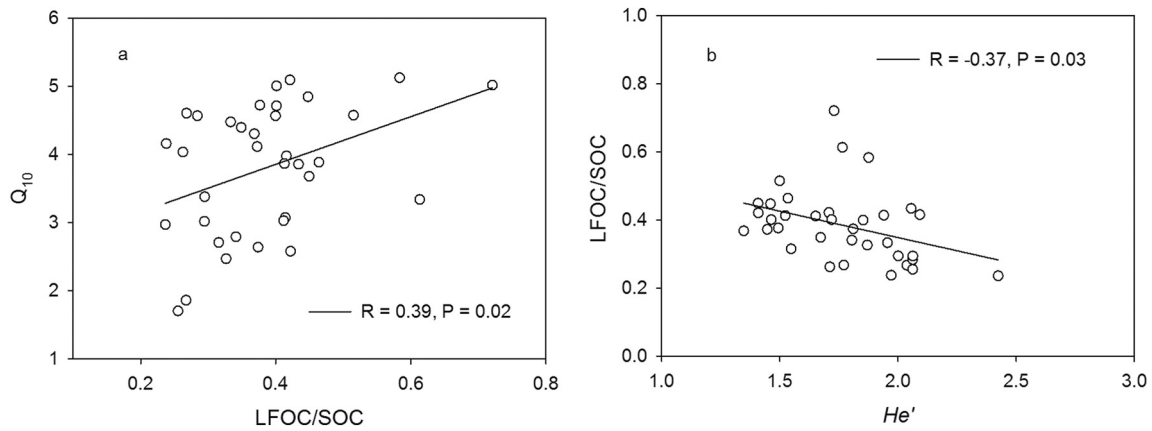


Fig. 3. Relationships a) between Q_{10} and LFOC/SOC, and b) between LFOC/SOC and He' for the broad-leaf stand ($r = 9$ m).

diversity indices for the broad-leaf stand (e.g., Fig. 3). Meanwhile, fine root (FR) biomass better illustrated the spatial variation of Q_{10} and was negatively correlated with the tree species diversity indices in the mixed stand (e.g., Fig. 4). On the other hand, for the mixed stand, subplots with more pine trees had higher Q_{10} values ($Q_{10} = 2.52 * N_{\text{pine}} / N + 3.3$, $R^2 = 0.14$, $P = 0.02$; N_{pine} : number of pine trees, N : the number of individuals of all species, $r = 9$ m, for example). There were also significant negative relationships between stand basal area (BA) and diversity indices (e.g., He') or richness (S) in the mixed rather than in the broad-leaf stand (Fig. 5).

4. Discussion

As an important ecosystem function, soil carbon sequestration has been linked to diversity of both aboveground vegetation (Wardle et al., 2012; Putten et al., 2013; Lange et al., 2015) and belowground soil microbes (Sulman et al., 2014; Lange et al., 2015; Tang and Riley, 2015), as well as competition between plant and decomposer (Averill et al., 2014). The stability of the soil carbon pool reflects one of the most important ecosystem characteristics in response to environmental perturbation. Evidences show that biodiversity increases the stability of ecosystem processes in response to environmental fluctuations (Tilman et al., 2006; Hector et al., 2010; Campbell et al., 2011), known as the diversity-stability relationship. In this study, we are the first to link the tree species diversity with one of the most important parameters of soil CO_2 flux in response to temperature fluctuation (i.e., Q_{10} value). Our results generally confirm our hypothesis, that subplots with a higher tree species diversity have lower Q_{10} values for both stands. This is corroborated by the positive relationship between Q_{10} and λ ,

and negative relationships between Q_{10} and He' , d and J_e . Moreover, the spatial variation of R_s is independent of tree species diversity, suggesting that tree species diversity benefits soil carbon stability by depressing the temperature sensitivity rather than by decreasing the rate of R_s . Both positive (Haren et al., 2013) and negative (Murphy et al., 2008) effects of tree species diversity on R_s have been reported in tropical plantations. In contrast to previous studies, we did not find significant effect of species diversity on R_s . Such contradictory results might be attributed to the different methods employed, where monoculture and mixed stands (Murphy et al., 2008; Haren et al., 2013) were employed to make comparisons in previous studies. While in this study, we employed the natural gradient of diversity that exists spatially in the studied stands and a linear regression was used to describe the relationship between diversity and R_s . Moreover, our results indicate that the correlation between diversity indices and Q_{10} is scale dependent, and the least area in which tree species diversity impacts soil process can be examined.

Species richness is a useful parameter in examining the effect of biodiversity on ecosystem properties (Campbell et al., 2011). Unexpectedly, species richness was neither significantly related with Q_{10} nor R_s . This might reflect the inherent difference between indices. Since we recorded all trees with DBH > 1 cm, one or two species with a small number of saplings may result in higher richness without a significant influence on ecosystem processes. If we only include trees with DBH > 10 cm, species richness was negatively correlated with Q_{10} for both the broad-leaf and the mixed stands. This indicates that caution should be taken when choosing biodiversity indices, especially when measured under diverse field conditions. Additionally, although different metrics have different meanings in describing

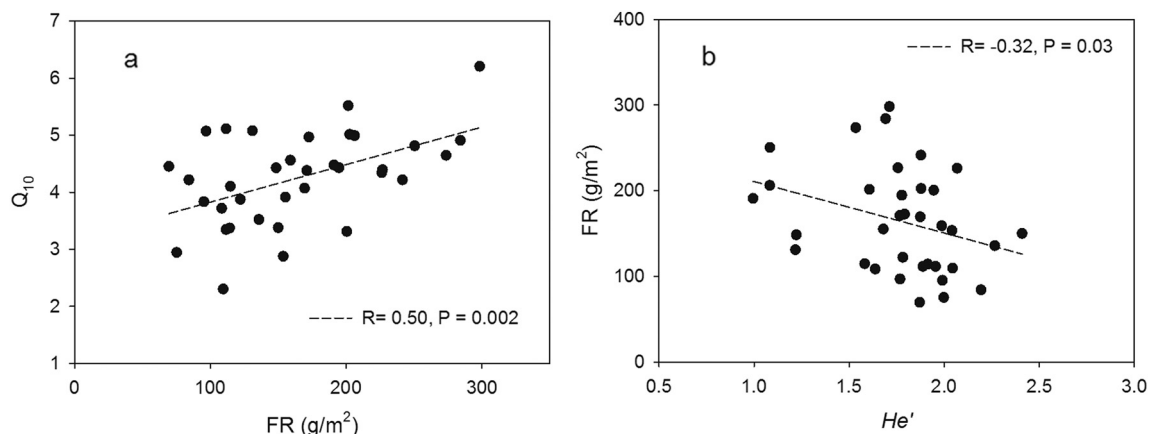


Fig. 4. Relationships a) between Q_{10} and FR, and b) between FR and He' for the mixed stand ($r = 10$ m).

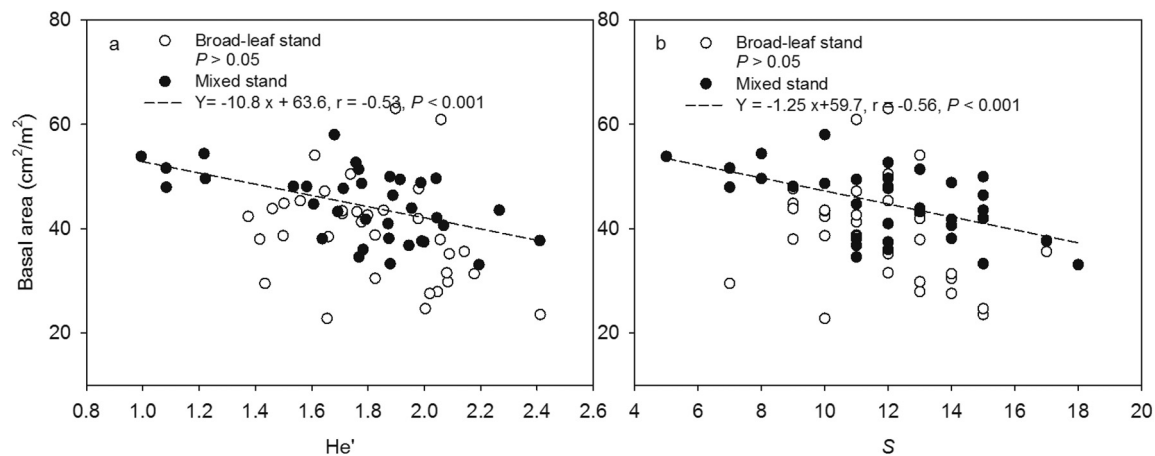


Fig. 5. Relationships between basal area and a) diversity indices (e.g., H_e') or b) species richness (S) for the broad-leaf and mixed stands ($r = 10$ m).

diversity, similar explanatory capacity was observed among the indices, thus our results confirmed that the diversity effect is generic rather than coincidental.

As we know, soil moisture has a large impact on soil respiration (Orchard and Cook, 1983), thus the observed effect of tree diversity on respiration might be mediated by different moisture regimes. Here, the positive correlations between soil moisture content and diversity (Table S1) suggest that diversity increased soil moisture content through decreasing evaporation by more closed canopy. Further, the negative correlations between SWC and R_s (Fig. S1a) suggest that the difference in soil moisture content contributed to some extent to the difference in soil respiration among subplots. Soil moisture content may not strongly regulate the Q_{10} as tree diversity did, the moisture content was within the optimum range for soil microbial activity most of the time in our study (e.g., 0.15–0.40 cm³ cm⁻³, Luan et al., 2011b; Luan et al., 2014). The above result is consistent with our previous study in this area, where the seasonality of soil respiration was not affected by soil moisture content, but was mainly affected by temperature (Luan et al., 2011a; Luan et al., 2011b).

The mechanisms for biodiversity to stabilize ecosystem properties still need to be further studied (Loreau and de Mazancourt, 2013), although three main mechanisms have been proposed (Loreau and de Mazancourt, 2013), including 1) the asynchrony of the species' intrinsic responses to environmental fluctuations, 2) differences in the speed at which species respond to perturbations, and 3) reduction in the strength of competition. Our results revealed that different mechanisms affect the biodiversity influence on soil organic carbon stability. For example, the reduction in competition may partly explain the stabilization effects of diversity on Q_{10} for the mixed stand, because negative correlations between FR biomass and diversity indices (e.g., H_e') were observed, in addition to a significant positive correlation between FR and Q_{10} . The negative relationships between BA, which can be a proxy for the intensity of competition (Paquette and Messier, 2011), and diversity indices or richness further confirm the abovementioned mechanism. However, similar phenomenon did not occur in the broad-leaf stand. Furthermore, the asynchrony of species' intrinsic responses to environmental fluctuations may also partly explain the effect of diversity on soil carbon pool for the mixed stand, because subplots having more pine trees had higher Q_{10} values due to different metabolism between evergreen coniferous and deciduous broad-leaf trees. A recent finding of the belowground carbon trading among tall trees in a temperate forest (Klein et al., 2016) suggests that high diversity causes a more complex trading network and leads to a more stable response of soil processes to environmental fluctuations.

In contrast, the mechanism of stabilizing effect of diversity on soil processes for the broad-leaf stand would be difficult to determine. Most studies show that the mass loss is often increased when litter of

different species is mixed (Gartner and Cardon, 2004; Handa et al., 2014). It in turn produces less labile organic matter, and the negative relationship between LFOC/SOC and H_e' is consistent with our finding in this study. It has also been illustrated that tree species could influence the magnitude and direction of microbial respiration during leaf litter decomposition (Makita and Fujii, 2015). Therefore, the significant positive correlation between Q_{10} and LFOC/SOC implies that the effect of tree species diversity on soil carbon stability in the broad-leaf stand may likely be more closely related to the quality of the substrate that is affected by tree species.

It is worth noting that soil respiration is composed of both heterotrophic respiration related to soil microbial activities, and autotrophic respiration or root respiration (Hanson et al., 2000). Here in our study we only studied total soil CO₂ efflux in evaluating its stability to environmental fluctuation. Part of the reason is that excluding roots to study heterotrophic respiration will exclude not only the root respiration, but also the important source of new carbon from root exudates (Lynch et al., 2013; Keiluweit et al., 2015), thus confound our understanding of how CO₂ efflux respond to environmental fluctuation. Nevertheless, how tree diversity impacts both heterotrophic and root respiration in response to environmental fluctuations is worth to be further studied, new methods or techniques, such as ¹³C₂ labeling, should be employed to elucidate this question.

In summary, our current study reveals that tree species diversity affects soil carbon stability by depressing the temperature sensitivity rather than the rates of R_s in two temperate forests. Our data suggest that there would be different underlying mechanisms between deciduous broad-leaf forest and coniferous-broad-leaf mixed forest. The exact mechanisms need to be further studied in rigorously-designed experiments, with more samples, and include different stand types and geographical locations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.07.036>.

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